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The Nucleus Premammillaris Ventralis (PMV) and Aggressive Behavior in the Rat

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Small bilateral electrolytic lesions placed just posterior of the ventromedial hypothalamic nucleus cause a strong increase in offensive behavior. The histology suggests that damage to the ventral premammillary nucleus is responsible for this effect. A summary of the neuroanatomical literature shows that this structure is connected to most other brain structures reported to be involved in offensive behavior.

Key words: aggressive behavior, mammillary bodies, lesions, rat

INTRODUCTION

Many studies on the central nervous organization of intraspecific aggressive behavior in rats have concentrated on various hypothalamic structures. Electrical stimulation of specific parts of the lateral hypothalamus enhance the probability of occurrence of aggressive behavior towards conspecifics [Woodworth, 1971; Panksepp, 1971; Koolhaas, 1978; Kruk et al, 1980]. Lesions in this same area reduce this behavior [Adams, 1971].

Lesions or local anaesthetic in the anterior part of the medial hypothalamus facilitate reactive fighting, whereas the same manipulations in the posterior part of the medial hypothalamus facilitate offensive aggression [Olivier, 1978; Albert and Wong, 1978]. Particularly in these lesion studies, it is difficult to assess exactly which brain structure is responsible for the observed behavioral effect. This is due to the fact that large lesions are generally used which damage many other brain structures.

However, in the interpretation of the increase in offensive behavior after posterior medial hypothalamic lesions, the ventromedial nucleus (VMH) was considered to be involved in this effect. This report will discuss that damage to a structure located just

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posterior to the VMH proper might be responsible for the dramatic increase in offensive behavior observed after medial hypothalamic lesions.

MATERIAL AND METHODS

Twenty-seven male rats of the strain WEzob (TNO breeding colony) of 300–350 g were used. Several weeks prior to the experiment, the animals were housed individually in large observation cages (80 × 60 × 50 cm) together with a sterilized female (ligation of the oviducts) in order to let them establish a territory. All animals were kept on a reversed day-night schedule, under constant temperature (20°C) and with ad libitum food and water available.

Lesions were made with a monopolar stainless steel electrode (Ø 0.2 mm) with a tapered bare tip of 0.1 mm. A dc anodal current of 750 μA for 10 seconds was used.

Procedure

After a few weeks habituation to the home cage (= observation cage), each experimental animal was tested three times in the presence of an unfamiliar male rat of a slightly lower weight and the same strain. As a rule, the resident experimental animal is dominant in such a situation. After these tests, eight animals were sham lesioned and the other 19 animals were lesioned bilaterally at the coordinates anterior 4.6, lateral 1.0, and ventral 4.0 [De Groot, 1963]. After a week of recovery from the operation, each animal was again tested daily for 3 days in the presence of a male intruder in its home cage.

After completion of the experiment, each animal was perfused with saline followed by 10% formaline. Frozen sections of the brain of 40 μm were cut and stained with cresylviolet.

Behavioral Recording

During each 10 minute test, a continuous record of the behavior of the experimental animal was made. A set of 20 behavioral elements was used, slightly modified after Grant and MacIntosh [1964] [see also Koolhaas et al, 1980]. These elements were defined such that the animal always performed one element at the time. From these records an offense, defense, and social exploration score was calculated; offense being the sum of the relative time spent in sideways posture, bite + kick attack, and keeping down; defense is the sum of upright posture and keeping off; and social exploration is the sum of investigating, social grooming, and genital sniffing.

RESULTS

A summary of the behavioral changes after the lesions is given in Table I. There is a significant increase in offensive behavior after the lesion, whereas defensive behavior did not change. The same changes can be seen in a comparison between lesioned animals and sham operated controls. In both the lesioned animals and the shams, social exploration decreased significantly. This may be due to a habituation to the repeated testing, since a between group comparison revealed no significant difference. In order to find out which anatomical structure might be responsible for the increase in offensive behavior, the lesioned animals were selected on the basis of the relative change in offensive behavior after the lesion. Figure 1 shows the result of this

TABLE I. Relative Time (± SEM) Spent on Various Social Behaviors Before and After PMV Lesions and Sham Operations

	Lesions			Shams			Sign[b]
	Before	After	Sign[a]	Before	After	Sign	Shams/Lesions
Offense	7.71 ± 1.42	17.52 ± 3.21	$p < 0.005$	11.27 ± 3.44	8.56 ± 2.66	NS	$p < 0.05$
Defense	4.42 ± 0.82	5.14 ± 0.97	NS	7.34 ± 1.84	5.22 ± 0.75	NS	NS
Social exploration	19.92 ± 1.31	10.92 ± 1.29	$p < 0.05$	16.35 ± 2.57	10.76 ± 2.73	$p < 0.01$	NS

[a]Wilcoxon Matched Pairs test; [b]Mann-Whitney U test.

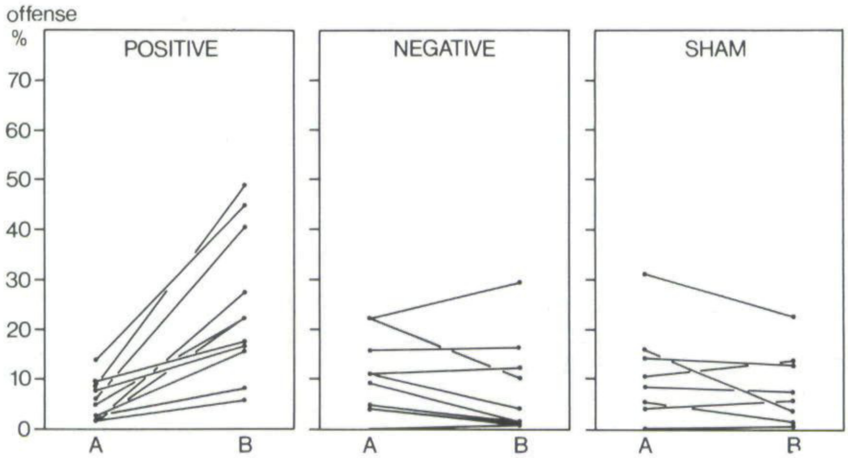

Fig. 1. Relative time spent on offensive behavior in lesioned and sham lesioned animals. Selection criterion for positive lesions was an increase of at least one and a half times preoperative level.

selection. Ten animals showed an increase in offensive behavior of at least one and a half times the preoperative level. These lesion sites were called positive. In nine animals, the lesion caused a change of less than this arbitrary chosen criterion. In fact, in some of these animals, a decrease of offensive behavior was observed. These lesion sites were called negative.

Figure 2 shows the histology of both the positive and the negative lesions. This figure also shows the histology of one animal as an example of a lesion almost restricted to the PMV resulting in a strong increase in offensive behavior. Most of the positive lesions have bilateral damage to the PMV in common.

The most offensive animals after the lesion tend to have the lesion restricted to the PMV itself, whereas the three positive animals with unilateral PMV damage showed the smallest increase in offensive behavior. Notice that the VMH remained intact in most of these animals. In the group with negative lesions, four lesions missed the

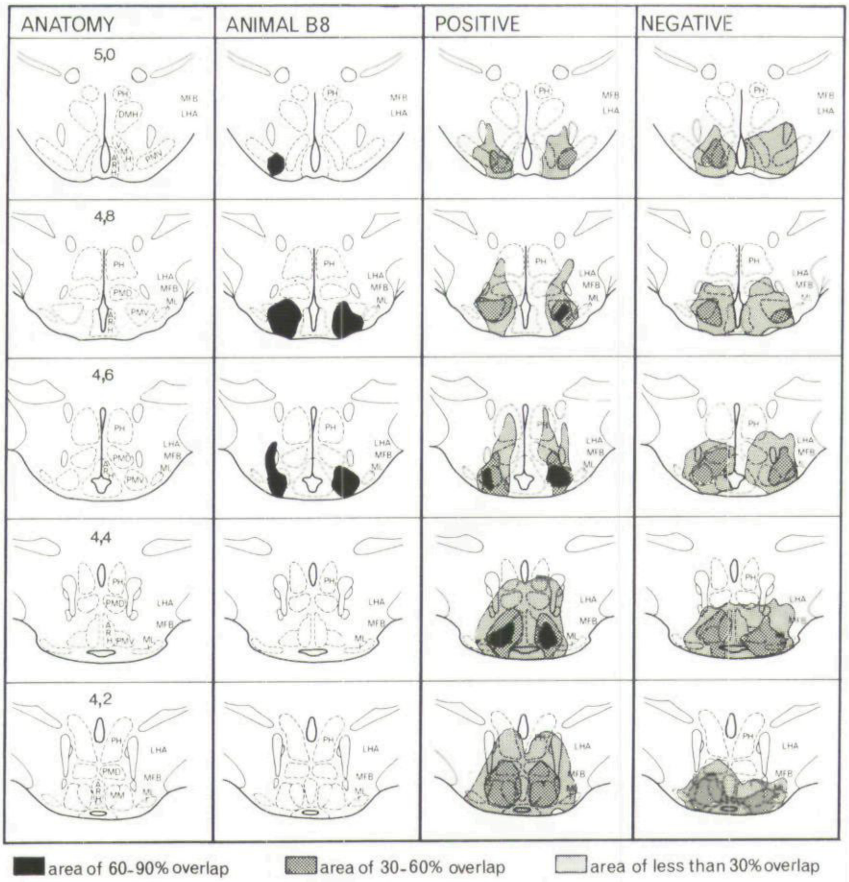

Fig. 2. Coronal sections of the rat hypothalamus [Pellegrino and Cushman, 1967] showing the lesion sites.

PMV completely, three lesions gave unilateral PMV damage, and two lesions were very large.

A more detailed analysis of the behavior of the three groups of animals is given in Fig. 3. The main behavioral change due to the positive lesion is an increase in sideways posture, keep down and clinch, whereas the upright posture is not influenced. The qualitative impression of the agonistic behavior of these animals is somewhat peculiar. Whereas intact animals usually terminate the agonistic interaction after a few clinches and keeping down the opponent, these lesioned animals continue to perform sideways posture throughout the experiment. It seems as if they get locked into some behaviors and have difficulty in terminating an agonistic sequence.

DISCUSSION

The data suggest that the strong increase in agonistic behavior after the lesion is due to bilateral damage to the ventral premammillary nucleus (PMV). It seems that this damage has to be restricted to this nucleus, since large lesions invading other

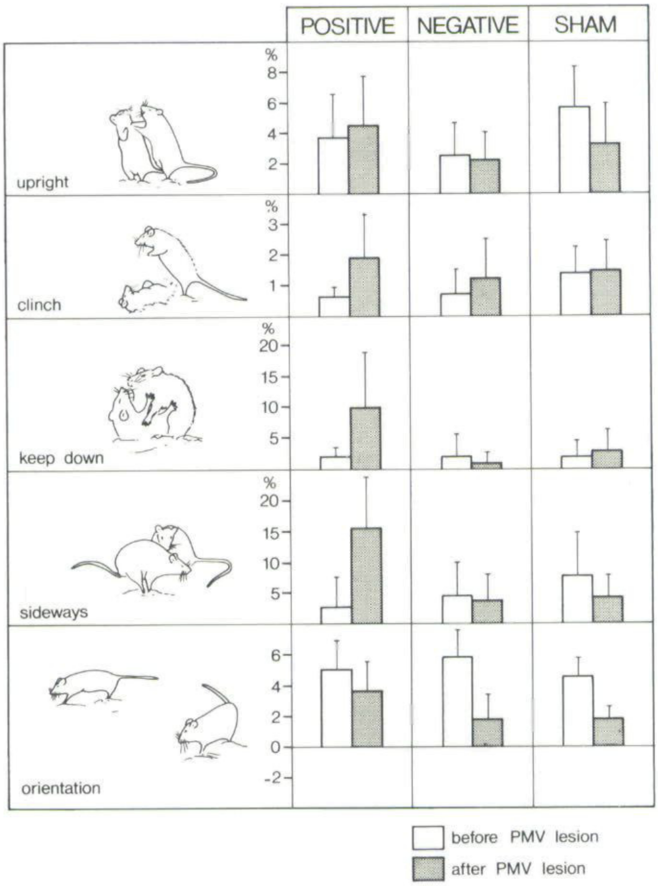

Fig. 3. Relative time spent on some behavioral elements for the three groups of experimental animals.

structures outside the PMV tend to result in no change or even a decrease in offensive behavior. Virtually no work has been done in the premammillary area. Grossman and Grossman [1970] and Paxinos and Bindra [1972] came closest to this area by making knife cuts in the caudal part of the medial hypothalamus. They reported that tube dominance and irritability did not change after these knife cuts. However, these data are difficult to relate to the results reported here, because of the different test situations used and the use of females instead of males. It seems likely that the increase in offensive behavior after posterior VMH lesions [Olivier, 1978] and local anaesthesia of this area [Albert and Wong, 1978] may be due to interference with the PMV.

The behavior of the PMV lesioned animals gives the impression that some kind of direction is lacking which normally determines the gross structure of an agonistic encounter. However, much more detailed behavioral analysis is necessary to establish the functional deficit created by these lesions. The deficit in spatial memory after mammillary body lesions reported by Rosenstock et al [1977] might be distantly related to this phenomenon.

Since the PMV is a completely neglected area in brain and behavior studies, it is relevant to summarize the neuroanatomical connections of this structure. The PMV

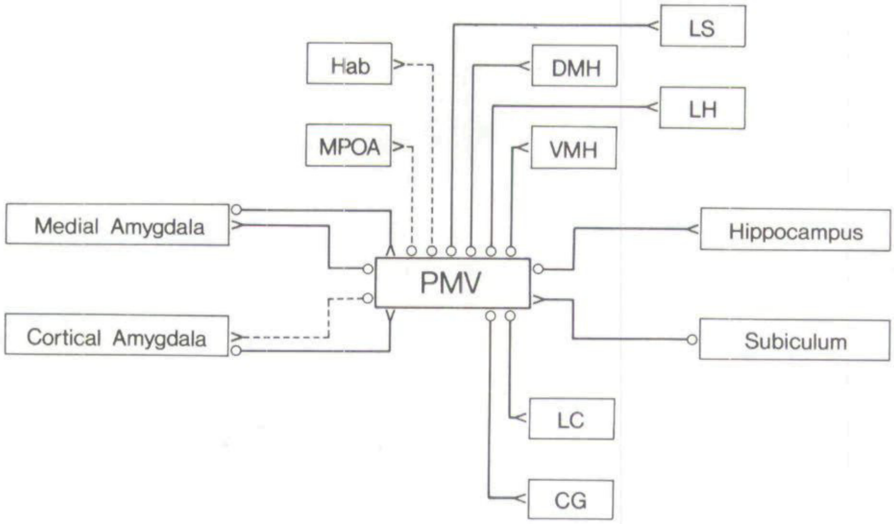

Fig. 4. Summary of the afferent and efferent connections of the PMV. Solid lines: literature data; broken lines: results of a preliminary silver degeneration study; CG: central grey; DMH: dorsomedial hypothalamus; Hab: habenula; LC: locus coeruleus; LH: lateral hypothalamus; LS: lateral septum; MPOA: medial preoptic area; VMH: ventromedial hypothalamus.

itself has never been the subject of a detailed neuroanatomical study. Hence, all information is gathered from studies on other brain structures. Figure 4 summarizes this information, and also includes some results of a preliminary silver degeneration study on small PMV lesions (broken lines). Krieger et al [1979] report efferent connections of the PMV with the hippocampus, lateral septum, and locus coeruleus. The connections with cortical and medial amygdala are reported by Veening [1978], Heimer and Nauta [1969], Lammers and Lohman [1974], Krettek and Price [1978], and McBride and Sutin [1977]. Finally, the hypothalamic efferents are reported in an HRP study by Luiten and Room [1980].

Although this neuroanatomical picture will be far from complete, it can be concluded that the PMV is connected to a variety of structures which are considered to be involved in aggressive behavior. It seems, therefore, that this structure must be taken into account in further studies on the central nervous organization of aggressive behavior.

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